Effects of silvicultural disturbance on acorn infestation and removal

Kenneth F. Kellner · Jeffery K. Riegel · Robert K. Swihart

Abstract Oak (*Quercus* spp.) regeneration is an important forest management goal in the central hardwood forest region of the United States. Silvicultural methods that target oak regeneration, such as the creation of canopy openings and removal of shade-tolerant midstory trees, are complicated by the impact of pre- and post-dispersal predators of oak acorns like acorn weevils (*Curculio* spp.) and granivorous small mammals. Understanding the effects of forest disturbance created by silviculture on these predators is important to promote successful oak regeneration. We conducted a 6-year study of acorn production, weevil infestation, and acorn removal at 113 black (*Q. velutina*) and white oak (*Q. alba*) trees impacted by three types of silvicultural treatments: adjacent to harvest openings, midstory removal (first-stage shelterwood harvest), and control (no harvest) in south-central Indiana, USA. We observed highly variable acorn production across years, but minimal impact of silvicultural treatments. Levels of weevil infestation and acorn removal by small mammal seed predators also varied greatly, and predation pressure was highest in years when acorns were scarce. Weevil infestation was reduced following midstory removal in shelterwood harvests, but probability of acorn removal by small mammals was unchanged following harvest. Damaged, germinated, and weevil-infested acorns were less likely to be removed by seed predators, suggesting additive effects of pre- and post-dispersal predators. This study emphasizes the importance of considering acorn predators in oak regeneration silviculture, and timing harvests to follow large acorn crops in order to reduce predation pressure and generate a high number of seedlings.

Keywords Oak · *Quercus* · Small mammals · Acorn weevils · *Curculio* · Acorn removal

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Introduction

Successful regeneration of desirable tree species is a core goal of sustainable forest management, either for economic (timber) reasons or to conserve the target tree species and associated flora and fauna. Depending on management objectives, various silvicultural techniques are used to shape the composition of forest stands by changing the structure of the forest to favor desirable species and discourage others (Daniel et al. 1979). A parallel management and conservation concern is how the disturbance created by silvicultural treatments will affect seed predators, which play a crucial role in the regeneration process and often are important parts of forest food webs themselves.

The oak (*Quercus* spp.) regeneration challenge in the central hardwood region of the midwestern United States (Fralish 2004) is a good example of the interaction of silviculture, tree regeneration, and the impact of seed predators. Oaks are an abundant and important overstory species group throughout central hardwood forests, valued for their timber and for their contributions to forest habitat (Fralish 2004; Ellison et al. 2005). Perhaps their most crucial contribution is the production of acorns, which are highly valued as food by at least 44 species of birds, small mammals, and larger vertebrates (McShea et al. 2007). Maintenance of oaks as a major component of the overstory is difficult, and oaks currently suffer regeneration failures throughout their range, likely due to changes in disturbance regimes that favor more shade-tolerant species (Abrams 2003). Mounting concern over these failures has prompted foresters to modify established silvicultural systems to more effectively promote oak regeneration (Dey 2002). In the central hardwoods, silvicultural prescriptions include the creation of canopy openings, from small gaps created by removing single trees (uneven-aged management) to large clearcut openings (even-aged management) within the stand. Very small openings are generally unsuitable for promoting oak regeneration because oak is outcompeted by advance regeneration of shade-tolerant species (Dey 2002). Large openings may also be unsuitable for oak regeneration where fast-growing species that out-compete oak, like yellow poplar (*Liriodendron tulipifera*), are abundant (Morrissey et al. 2008). Shelterwood systems, in which canopy removal occurs in phases rather than all at once, provide an alternative method to promote oak regeneration. The gradual reduction in canopy density creates an intermediate light regime conducive to the establishment of competitive advance oak regeneration prior to complete overstory removal (Loftis 1990; Schlesinger et al. 1993; Dey 2002).

In addition to light availability and other factors manipulated by silvicultural treatments, seed predators can be a crucial factor that limits the establishment of new oaks. Acorns suffer significant pre-dispersal mortality due to infestation by insects, including gall wasps (Hymenoptera: Cynipidea), acorn moths (Lepidoptera: Oleuthreutidae), and acorn weevils (Coleoptera: Curculionidae). As many as 50–90 % of acorns may be infested by acorn weevils each year (Marquis et al. 1976; Gribko 1995; Riccardi et al. 2004; Lombardo and McCarthy 2008), and infested acorns are less likely to be dispersed by mammals (Hadj-Chikh et al. 1996) and less likely to germinate (Andersson 1992; Lombardo and McCarthy 2009). Acorns also are subjected to post-dispersal mortality from vertebrate seed predators. In the central hardwood forest region, acorns are a primary food source for white-tailed deer (*Odocoileus virginianus*), birds, and small mammals such as the gray squirrel (*Sciurus carolinensis*; McShea et al. 2007). High levels of acorn predation have contributed to the general failure of direct seeding methods for oak (Dey et al. 2008). Of course, acorn removal by predators does not guarantee mortality; some predators (e.g., *S. carolinensis*) cache rather than immediately consume acorns, promoting germination success if the caches are not recovered (Barnett 1977; Smallwood et al. 2001; Steele et al. 2006).

The habitat disturbance created by silvicultural treatments potentially alters acorn production and sources of pre- and post-dispersal acorn mortality, with consequences for the establishment of oak seedlings important for successful regeneration. Both edge habitat and midstory removal increase light availability for the remaining canopy oaks, which may increase branch density and therefore acorn production (Verme 1953; Johnson 1994). Thinned stands (e.g., partially harvested or mid-shelterwood), harvest openings, and edges have higher soil moisture than interior forest (Minckler et al. 1973; Harpole and Haas 1999; Ritter et al. 2005), possibly influencing the distribution of acorn weevils that are sensitive to soil moisture (Menu 1993; Ricca et al. 1996). Increases in understory vege-tation at edges or following midstory removal may provide cover and thus facilitate increased seed predation by mammalian seed predators (Pérez-Ramos and Marañón 2008). Finally, the abundances of several small mammal seed predators are altered by timber harvest (e.g., Kirkland 1990; Kellner et al. 2013). Changes in the behavior or abundance of pre- and post-dispersal acorn predators following silvicultural treatments could have important implications for successful oak regeneration, particularly in shelterwood har-vests designed to enhance the establishment of advance oak regeneration. A few studies have examined the effects of silvicultural treatments including thinning, burning, and shelterwood harvesting on red oak (*Q. rubra*), black oak (*Q. velutina*), and chestnut oak (*Q. prinus*) acorn production and seed predators in eastern forests (e.g., Bellocq et al. 2005; Lombardo and McCarthy 2008), but further study in different regions and with additional common oak species is necessary to elucidate general patterns.

We examined changes in black oak and white oak (*Q. alba*) seed production and predation due to two types of forest disturbance caused by silvicultural treatments: (1) the creation of an edge adjacent to a clearcut opening, and (2) midstory tree removal as the first phase of a shelterwood harvest. Specifically, our study addressed the effects of these treatments on (1) acorn production, (2) probability of acorn infestation by weevils, and (3) probability of acorn removal by seed predators.

Methods

Study area and design

All experiments were conducted in Morgan–Monroe State Forest, Yellowwood State Forest, and Brown County State Park, Indiana, USA, comprising >18,000 ha of forest in total across three Indiana counties. The three forests are similar and are characterized by uplands underlain with silt-loam soils and steep slopes ranging from 23 to 35 % (Indiana Department of Natural Resources 1984; Jenkins and Parker 1998). Annual mean temper-ature is 13–16 °C and mean precipitation is 112–137 cm (McNab and Avers 1994). The overstory is dominated by oak and hickory (*Carya* spp.); sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) are common in the understory and midstory (Saunders and Arseneault 2013). Basal areas before harvest ranged from 21.7 to 29.9 m²/ha, and total tree density ranged from 923 to 1,527 trees/ha (Saunders and Arseneault 2013). Morgan–Monroe and Yellowwood State Forests are managed for multiple uses, including recreation, conservation, and timber. Past timber harvests consisted mainly of group and single-tree selections (Jenkins and Parker 1998; Carman 2013).

In 2006, the Hardwood Ecosystem Experiment, a long-term study of the effects of silvicultural systems to regenerate oak on forest ecosystems, was established within these forests. Ten research cores (83.4–110.9 ha) were delineated within the three properties and

assigned one of three timber management regimes: even-aged (4 ha clearcuts and shelterwood harvests), uneven-aged (0.4–2 ha patch cuts and single-tree selection), and no harvest (Kalb and Mycroft 2013). In patch cuts and clearcuts, all trees with d.b.h. > 1 cm were removed through a combination of harvest and timber stand improvement (TSI); TSI consisted primarily of cutting stems left after harvest and a small amount of girdling. The shelterwood harvest consists of three phases: first, removal of non-oak trees <25.4 cm d.b.h. (i.e., midstory trees) down to a minimum residual basal area of 13.8 m^2/ha, followed by an establishment cut 5–10 years later reducing basal area to 13.8–16.1 m^2/ha, and finally by removal of remaining overstory trees 15–20 years after the initial cut (Kalb and Mycroft 2013).

In August 2006, 3 years before harvests, 57 black oak and 56 white oak trees were selected for inclusion in the study. Trees were either (1) on the edge of future clearcuts or patch cuts ($n = 31$), (2) within future shelterwood harvests ($n = 18$), or (3) located randomly within the unharvested control areas ($n = 64$). Following 3 years of pre-treatment data collection (2006–2008), timber harvests were implemented between November 2008 and March 2009. Following harvest, trees were assigned to one of three forest disturbance treatments corresponding to their locations: (1) "opening edge" treatment for trees adjacent to clearcuts and patch cuts, (2) "midstory removal" treatment for the trees within shelterwood harvests (as only the midstory removal phase occurred in 2009), and (3) "control" treatment for trees in unharvested areas.

Tree characteristics were measured in 2011. The diameter at breast height (d.b.h), height, length of the live crown, and crown area of each tree were measured. Height measurements were taken using a hypsometer (Vertex IV, Haglöf Inc.). Eight crown radius measurements (in the cardinal and intercardinal directions) were taken from the trunk of the tree to the drip line, and crown area was estimated as the area of the octagon created by the resulting points (Greenberg 2000).

Acorn production

To measure acorn production, two acorn collection traps were established beneath the crown of each tree. Traps were made of 52 × 33 × 32 cm plastic bins mounted on 2 m high PVC pipes driven into the ground. A total of 0.34 m^2 was sampled by traps underneath the crown. Traps were covered with 3.8 cm chicken wire, which allowed acorns to fall into the bin but denied access to squirrels and other acorn predators. Traps were opened in late August and visited 5–8 times during the months of September through December of each year of the study. All mature acorns collected were identified to species, counted, and removed during each visit.

Acorn infestation

Acorns collected in traps for measurement of production (section "acorn production") were examined to determine if they were infested with acorn weevils (*Curculio* spp.). Acorns were marked according to source tree and X-rayed in groups of 50 using a Specimen Radiography X-ray System (Faxitron X-ray Corporation, Lincolnshire, IL). Typically, weevil-damaged acorns show characteristic dark patches on X-ray film (Dixon et al. 1997; Lombardo and McCarthy 2009). Acorns were classified as 'infested' if any portion of the acorn interior exhibited weevil damage.

Acorn removal

To separate the contributions of several seed predators to the process of acorn removal, a set of 4 semipermeable exclosures was established on the ground beneath the crown of each tree. Each square exclosure covered 0.56 m². The first 'exclosure' was simply open ground marked at the 4 corners with wooden stakes, allowing access to all acorn predators. The second exclosure consisted of 4 wooden stakes covered on the top and sides by 3.8 cm wide hexagonal chicken wire, denying access to deer and turkey (*Meleagris gallopavo*). The wire began 15 cm above the ground, allowing access by squirrels and smaller seed predators. The third exclosure consisted of a 0.56 m² wooden frame with a height of 0.2 m, covered in 3.8 cm chicken wire. This exclosure denied access to squirrels and larger wildlife but allowed access by mice (*Peromyscus leucopus*). The final control exclosure was a wooden frame of the same size as the previous exclosure, but was instead covered by 0.6 cm mesh hardware cloth to deny access to all vertebrates.

The four exclosures were arranged randomly underneath the tree crown. Acorns were allowed to fall naturally into the exclosures to reflect ambient acorn availability. Because the narrow hardware cloth mesh prevented acorns from falling into the control exclosure, a number of acorns from beneath the tree equal to the mean of the number within the other three exclosures were manually inserted into the control exclosure. Each tree was visited 5–8 times in the months of September–December of each study year. On each visit, acorns that had fallen into the exclosures were numbered using a black marker. Characteristics were recorded for each marked acorn, including species, germination state, the presence/absence of weevil exit holes, and an assessment of acorn integrity (i.e., broken/damaged or intact). On subsequent visits, the presence or absence of the acorn in the exclosure was recorded to yield an encounter history. If the acorn was still present, any changes in its characteristics were also recorded.

Analysis

Tree characteristics (height, d.b.h., and crown area) were compared among disturbance treatments and species using two-way analysis of variance in R (R Foundation for Statistical Computing, Vienna, Austria). Acorn production, weevil infestation, and acorn removal were modeled separately using hierarchical generalized linear mixed models. Each model considered research core ($n = 1$–10), tree ($n = 1$–113), and year ($n = 1$–6) as random effects, with a hierarchy of years nested within trees, and trees nested within cores. Differences among yearly acorn production (pooled across treatments) were compared using non-parametric multiple comparisons according to Siegel and Castellan (1988) in R.

Acorn counts were summed within each year, yielding a total count of acorns collected in the months of September-December. Counts were modeled as a Poisson random variable with parameter λ_{jkt}, the mean acorn count for tree j in research core k and year t. Tree height, d.b.h., d.b.h. centered on the mean and then squared, species (black or white oak) and disturbance treatment (opening edge or midstory removal) were considered as fixed-effect covariates on the tree-level mean count.

The infestation status of an individual acorn i (0, uninfested, or 1, infested) was modeled using logistic regression as a Bernoulli random variable with parameter p_{jkt}, the probability of infestation for an acorn from tree j in core k and year t. Tree species, disturbance treatment, and the total number of collected acorns at tree j in year t were considered as fixed effect predictors of the tree-level mean probability of infestation. Tree d.b.h. and height did not have an important effect on removal probability, consistent with our

expectation that variation in these tree characteristics was unlikely to impact the behavior of nearby seed predators. Thus, they were not included in the model.

For each acorn i from tree j, core k, and year t included in the removal study, we generated an encounter history that began at the sampling occasion l ($n = 5$–8) when the acorn was first observed and ended either on the sampling occasion in which it was no longer observed inside an exclosure or at the conclusion of the sampling occasions in each study year. We modeled an acorn's probability of remaining in an exclosure between occasion l and occasion $l + 1$, Φ, as a Bernoulli random variable. Silvicultural disturbance type was included as a predictor of tree-level mean Φ, and acorn species, exclosure type, germination status, acorn integrity (broken or intact), and the presence of weevil exit holes were considered as predictor variables at the individual observation level of the model. We also simultaneously tested for differences between each pair of parameters associated with exclosure type. Though we modeled acorn retention in exclosures, we were truly interested in the effect of covariates on the probability of removal, equal to $1 - \Phi$. Therefore, to facilitate easier interpretation, we reversed the signs of the estimated parameter values to reflect their effects on acorn removal instead of retention.

All models were fit in a Bayesian framework using the program WinBUGS (Spiegel-halter et al. 2003), called from within the software package R (R Foundation for Statistical Computing, Vienna, Austria) using the R2WinBUGS library (Sturtz et al. 2005). Win-BUGS uses Markov chain Monte Carlo (MCMC) techniques to generate entire posterior distributions for model parameters. Convergence of MCMC chains was assessed with the diagnostic Rhat (Brooks and Gelman 1998), and posterior predictive checks were performed for all models to insure adequate fit. Continuous covariates were standardized prior to analysis. Individual parameters were considered to be important if the 95 % credible interval around the parameter estimate did not include 0.

Results

Tree characteristics

There were no significant differences among treatments for tree height ($F = 1.273$, $p = 0.28$), d.b.h. ($F = 1.582$, $p = 0.21$), or crown area ($F = 2.884$, $p = 0.06$). There were no significant differences for these variables between oak species either ($F = 0.748$, $p = 0.39$; $F = 3.763$, $p = 0.06$; and $F = 0.004$, $p = 0.95$ for height, d.b.h., and crown area respectively), or for the interaction of species and treatment ($F = 1.124$, $p = 0.33$; $F = 2.56$, $p = 0.08$; $F = 1.11$, $p = 0.33$ respectively). Across all treatments and species, mean tree height ($\pm$standard error) was 30.34 ± 0.43 m, mean d.b.h. was 50.39 ± 4.76 cm, and mean crown area was 109.22 ± 10.32 m^2.

Acorn production

Mean acorn production (per m^2 crown area) by both black and white oaks varied greatly over the 6 years of the study (Fig. 1), with at least 2 years of poor mast production for each species (2008 and 2009 for black oak; 2009 and 2011 for white oak). Similar amounts of variation in production were explained by the year and tree levels of the mixed model, with a smaller amount of variation explained by differences among research cores (Table 1). White oak production was unaffected by both treatments, but production by black oaks on

opening edges was reduced (Table 1). There was little evidence of a relationship between tree d.b.h. and acorn production for the range of tree sizes in our study (Table 1).

Weevil infestation

A total of 2,118 acorns were X-rayed to determine weevil infestation status. Overall, the mean proportion of infested acorns across both oak species varied greatly by year from a minimum of 0.11 [95 % confidence interval (CI) 0.08–0.14] in 2006 to a maximum of 0.93 (CI 0.84–1.00) in 2009. The highest levels of infestation occurred in 2008 and 2009 for both black and white oak, and also in 2011 for white oak, corresponding with years of mast failure in those species (Figs. 1–2). Accordingly, more variation in the mixed model was explained by the random effect of year than by research core or tree (Table 2). The midstory removal treatment decreased the probability of acorn infestation (0.18, CI 0.12–0.24) relative to the control treatment (0.30, CI 0.26–0.34) in the years following harvest and this difference was important based on the mixed model (i.e., the 95 % credible interval around the parameter estimate did not include 0; Table 2). Likewise, a lower proportion of white oak acorns were infested (0.19, CI 0.16–0.22) than black oaks (0.22, CI 0.19–0.24), and this difference was also important based on the model (Table 2).

Acorn removal

In total, 6,244 acorns were monitored for removal by predators during the study. Across all years, species, and exclosure types, the proportion of acorns removed from exclosures was 0.43 (CI 0.42–0.44). Among acorns accessible to at least some vertebrates (i.e., excluding the inaccessible control exclosure), the proportion was 0.55 (CI 0.53–0.56). Proportions of removed acorns varied greatly among years in the study, from a minimum of 0.31 (CI 0.28–0.34) in 2006 to a maximum of 0.60 (0.54–0.67) in 2008 (Fig. 3). As with weevil infestation, the proportion of removed acorns was highest in years of low mast production (Fig. 1). The random effects of tree and year explained a similar amount of variation; both explained more variation than the random effect of research core based on the mixed model (Table 3). Neither disturbance treatment had a strong effect on probability of removal (Table 3). Several acorn characteristics affected removal probability; acorns that were weevil-infested, damaged, or germinated were less likely to be removed than intact acorns, but species had no effect (Table 3). Probability of removal also decreased later in the season (Table 3). The proportion of removed acorns differed among exclosure types, with the greatest proportion removed from the exclosure that allowed access to squirrels and smaller vertebrates, followed by the exclosure that allowed access to all animals and the exclosure that allowed access only to mice and chipmunks (Fig. 3; Table 3). Contrasts between all pairs of exclosure types were different from zero based on the model (Table 3).

Discussion

Acorn production

Production of acorns per unit of crown area in this study varied greatly among years. Previous work also found acorn production by black and white oaks to be highly variable from year to year (Downs and McQuilkin 1944; Sork et al. 1993; Cecich and Sullivan
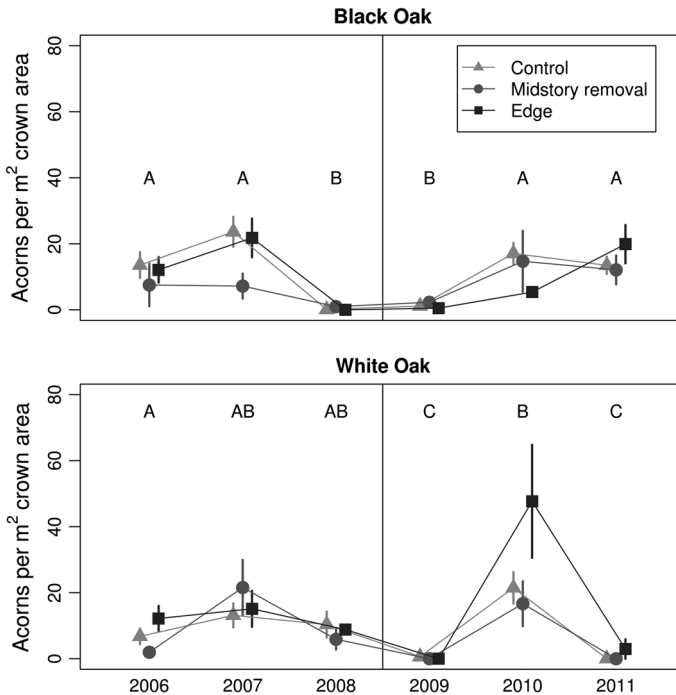
Fig. 1 Mean acorns produced per square meter of crown area over a 6-year period, by oak species (black oak; *Quercus velutina*, and white oak; *Q. alba*) and silvicultural disturbance treatment (control, opening edge, midstory removal). Harvests occurred between 2008 and 2009 measurements. *Error bars* represent standard errors around the mean. Significant differences among yearly mean production for each species (pooled across treatments) were identified using non-parametric multiple comparisons (Siegel and Castellan 1988) and are indicated by *different letters*

1999; Lombardo and McCarthy 2008). Acorn production by the two tree species exhibited a degree of synchrony, with good production from both species in 2007 and 2010 and poor years in 2008 and 2009. White and black oaks require a different number of years for acorns to mature (1 and 2 years, respectively), and previous work has reported asynchrony between oaks with different time requirements for acorn maturation (Koenig and Knops 2002). However, Liebhold et al. (2004) identified a weak positive correlation in acorn production between black and white oaks. Synchronized production from these two species could negatively affect wildlife that rely on mast as a food source because years of poor production from each species would often coincide. However, other sources of hard mast are present at our sites, including other oak species (notably chestnut oak) and hickories, which may be asynchronous with black and white oak.

Neither silvicultural treatment had an effect on acorn production by individual trees of either oak species (Table 3). In the midstory removal (shelterwood) stands, this is not surprising since only midstory trees were removed in this treatment, with little effect on light availability for dominant oaks in the canopy. Other studies have also failed to find strong evidence that thinning (by itself or as part of a shelterwood harvest) increases acorn production. Mean production in red oak was higher in thinned stands in Massachusetts, but the difference was not significant (Healy 1997). Bellocq et al. (2005) removed a greater portion of stand basal area than in this study and found a difference in production between

Table 1 Output from generalized linear mixed models of acorn production by black oak (*Quercus velutina*) and white oak (*Q. alba*), showing variation explained by each random effect as well as estimates of covariate effects and the 95 % credible interval around those estimates

Species	Black oak		White oak	
Parameter	Estimate	95 % CI[a]	Estimate	95 % CI[a]
Random effects				
Core-level variation[b]	0.35	0.03 to 0.82	0.51	0.10 to 1.10
Tree-level variation[b]	1.54	1.33 to 1.81	1.72	1.47 to 1.99
Year variation[b]	2.29	1.07 to 5.00	2.29	1.53 to 4.69
Fixed effects				
Opening edge effect	−0.81[c]	−1.58 to −0.07	0.16	−0.77 to 1.13
Midstory removal effect	−0.15	−1.26 to 0.90	0.37	−0.65 to 1.33
Tree d.b.h.	0.25	−0.05 to 0.56	0.23	−0.16 to 0.57
Tree height	−0.08	−0.32 to 0.17	0.24	−0.07 to 0.53

All continuous covariates were standardized

[a] Credible interval (Bayesian analogue to confidence interval)

[b] Standard deviation of the distribution of random effects

[c] Parameter is statistically different from 0; i.e., 95 % credible interval does not overlap 0

red oaks in a shelterwood harvest and control trees using visual counts, but not based on collection buckets in the same stands. Lombardo and McCarthy (2008) reported an increase in chestnut oak production following thinning but no difference in black oak production. Healy (1997) examined years 3–9 following thinning treatment and also failed to find a significant difference in production. In contrast, Lombardo and McCarthy (2008) detected a difference in chestnut oak in years 1–5 following thinning.

For oaks located on opening edges, the removal of surrounding trees should increase the amount of light reaching the crown, which is correlated with levels of acorn production (Verme 1953; Johnson 1994). However, we observed no change in production by white oaks on the edge of openings. Production by black oaks was actually reduced after harvest openings were created. Our results suggest that 3 years post-harvest may be insufficient time for trees along openings to translate increased light into increased acorn production. Regardless, the year-to-year differences in production by both species dwarfed any changes in production due to silvicultural treatment.

Weevil infestation

We observed reduced probabilities of weevil infestation in acorns from trees occupying midstory removal stands, and marginally lower infestation on opening edges. Multiple factors could contribute to the reduced probability of infestation we observed in these treatments. Moisture conditions change considerably following silvicultural treatments (Zheng et al. 2000). Weevils are sensitive to soil moisture conditions; adult chestnut weevils (*C. elephas*) were less likely to successfully emerge from the soil when moisture was low (Menu 1993), but overwinter survivorship of *Curculio* larvae was negatively related to soil moisture (Ricca et al. 1996). Partial harvests can result in higher soil moisture than in intact forest (Harpole and Haas 1999). Higher winter soil moisture in stands with no midstory may therefore reduce survivorship of weevil larvae (Ricca et al. 1996), explaining the reduction in
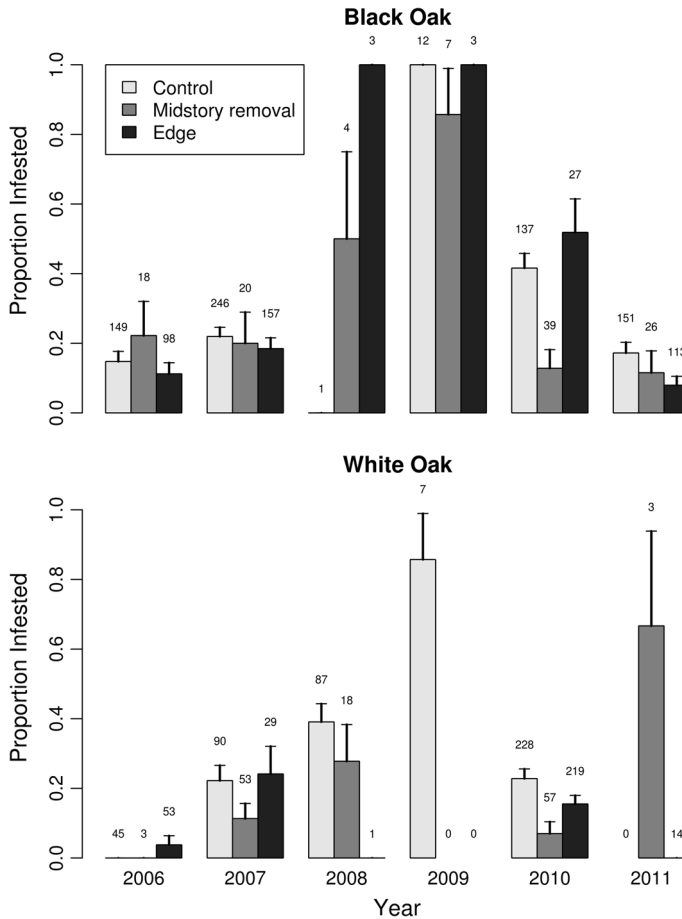
Fig. 2 Proportion of black oak (*Quercus velutina*) and white oak (*Q. alba*) acorns infested with weevils (i.e., showing weevil damage when X-rayed), by year and silvicultural disturbance treatment (control, opening edge, midstory removal). Harvests occurred between 2008 and 2009 measurements. *Error bars* represent standard errors around the mean, and the numbers above each column represent sample size

overall infestation probability we observed. In our study, the removal of just midstory trees likely did not strongly increase soil moisture because dominant canopy trees, which require much more water, remained. Therefore, an alternative but not mutually exclusive explanation is that the reduced density of trees in harvested stands disrupts successful weevil dispersal; they are considered poor dispersers (Menu and Debouzie 1993). However, only non-oak trees were removed during the shelterwood harvest, so the distribution of potential host trees for dispersing weevils was likely unchanged. Previous studies in similar forests failed to find differences in weevil infestation of acorns in thinned and control stands (Bellocq et al. 2005; Lombardo and McCarthy 2008), though Healy (1997) observed that infestation was marginally lower in thinned red oak stands. These inconsistent results could also be due to differences in the intensity of thinning between studies; as noted in "Acorn production" section, the roughly 20 % of basal area removed in the shelterwood harvest was lower than the range reported by other studies (30–85 %; Healy 1997; Bellocq et al. 2005;

Table 2 Output from generalized linear mixed model of acorn infestation by weevils (*Curculio* spp.), showing variation explained by each random effect as well as estimates of covariate effects and the 95 % credible interval around those estimates

Parameter	Mean	95 % credible interval
Random effects		
Core-level variation[a]	0.09	0.03 to 0.28
Tree-level variation[a]	0.61	0.42 to 0.83
Year variation[a]	2.27	1.04 to 4.81
Fixed effects		
Opening edge effect	−0.38	−0.84 to 0.07
Midstory removal effect	−0.96[b]	−1.75 to −0.33
Acorn species (white oak = 1)	−0.70[b]	−1.02 to −0.38
Local acorn availability (index)	−0.05[b]	−0.09 to −0.01

All continuous covariates were standardized

[a] Standard deviation of the distribution of random effects

[b] Parameter is statistically different from 0; i.e., 95 % credible interval does not overlap 0

Lombardo and McCarthy 2008). Differences in forest composition could also play a role; our sites were characterized by a combination of black, white, chestnut, and red oaks whereas both Healy (1997) and Bellocq et al. (2005) were working in stands dominated by red oak.

Harvest openings also have greater soil moisture than the forest interior (Minckler et al. 1973; Harpole and Haas 1999), and edges may have even higher soil moisture (Ritter et al. 2005). However, we did not observe differences in weevil infestation among acorns collected from edge trees. Little information is available on weevil responses to edge habitat, but in Indiana woodlots surrounded by agricultural fields, Govindan et al. (2012) also found no difference in weevil occupancy between edge and interior oak trees.

Overall, levels of weevil infestation in this study are comparable to those reported in similar regions and oak species. In years of good acorn production, infestation ranged from 13 to 37 % for black oak and 2–37 % for white oak. Lombardo and McCarthy (2008) reported 68 % infestation for black oak and 26 % for chestnut oak in good mast years, and Healy (1997) reported 20–25 % infestation in red oak. Maximum infestation occurred in years of mast failure when resources were scarce for emerging adult weevils. Accordingly, variation in infestation among years was much greater than among research cores or individual trees. This relationship was similar at a finer spatial scale; weevil infestation was negatively correlated with the number of available acorns at the scale of individual trees. Superficially, this provides evidence of the predator satiation hypothesis (Janzen 1971; Silvertown 1980): during years of mast abundance many acorns escaped infestation. According to this hypothesis, 'bust' or mast failure years are part of an evolved strategy to starve seed predators between masting events and keep their populations in check (Silvertown 1980). However, in our study infestation was similar before and after the mast failure period (2008–2009). In 2010 infestation exceeded pre-mast failure levels rather than being temporarily reduced following the resource deficiency. Weevil populations may have been maintained by other oak species at our sites such as chestnut oak, which we did not monitor and which may not have exhibited synchrony in mast production with black and white oaks (Govindan et al. 2012). In addition, weevils can undergo a prolonged diapause of 2-3 years in the soil, undermining the predator satiation strategy (Maeto and Ozaki 2003).
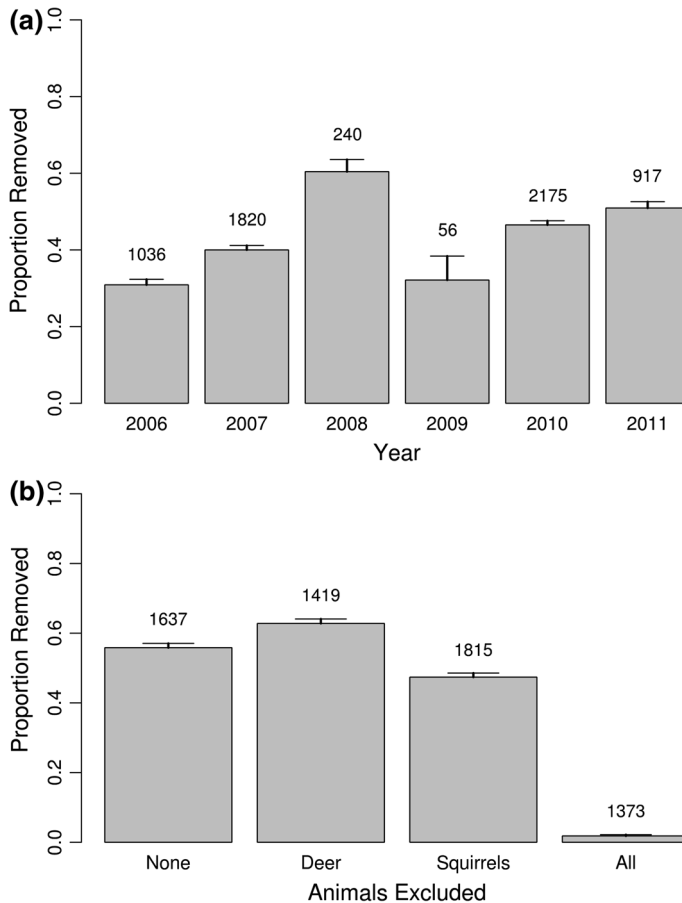
Fig. 3 Proportion of tracked acorns (both *Quercus velutina* and *Q. alba*) removed **a** by study year and **b** by exclosure treatment. Exclosure treatments prevented access to acorns by all vertebrates ("All"), squirrels and larger animals ("Squirrels"), deer, turkeys, and other large animals ("Deer"), and no animals ("None")

Black oak acorns were more likely to be infested than white oak acorns. The assemblage of *Curculio* species at our study sites likely plays a role, because some weevil species specialize on particular species of oak (Gibson 1972; Gibson 1982). There also is some evidence that black oak may be a more consistent mast producer than white oak (Sork et al. 1993), allowing the black oak population to support a larger number of weevils at our sites; however, our study does not provide strong evidence of a difference in production or variation between the oak species. Our results agree with those of Lombardo and McCarthy (2008), who found higher rates of infestation in black oak than in chestnut oak (which belongs to the white oak group) in southeastern Ohio.

Removal by predators

Pressure from vertebrate acorn predators was high. Fifty-five percent of monitored acorns were removed over the course of the study. As with weevil infestation, removal was

Table 3 Output from generalized linear mixed model of acorn removal by granivorous small mammals, showing variation explained by each random effect as well as estimates of covariate effects and the 95 % credible interval around those estimates

Parameter	Estimate	95 % credible interval
Random effects		
Core-level variation[a]	0.20	0.01 to 0.51
Tree-level variation[a]	1.19	1.07 to 1.33
Year variation[a]	0.98	0.43 to 2.13
Date and treatment parameters		
Opening edge effect	0.20	−0.27 to 0.72
Midstory removal effect	−0.17	−0.81 to 0.52
Julian date	0.16[c]	−0.09 to 0.23
Time between samples	0.36[c]	0.32 to 0.39
Effect of acorn characteristics		
Acorn species	0.27	−0.015 to 0.55
Weevil infestation	−0.97[c]	−1.20 to −0.75
Germination status	−0.40[c]	−0.69 to −0.14
Broken/damaged	−0.50[c]	−0.75 to −0.31
Exclosure type parameters		
Open exclosure	4.54[b, c]	4.41 to 4.95
Deer & larger excluded	4.75[b, c]	4.37 to 5.11
Squirrel & larger excluded	4.01[b, c]	3.66 to 4.39
Open relative to deer exclosure	−0.20[b]	−0.32 to −0.08
Deer relative to squirrel exclosure	0.73[b]	0.61 to 0.85

All continuous covariates were standardized

[a] Standard deviation of the distribution of random effects

[b] Relative to the control exclosure which denied access to all vertebrates

[c] Parameter is statistically different from 0; i.e., 95 % credible interval does not overlap 0

maximized in a year of low acorn availability (2008). Silvicultural treatments had no impact on acorn removal. A related study at these sites found that herbaceous and woody understory cover and coarse woody debris increased following shelterwood harvest and in clearcut openings/edge habitat (Kellner et al. 2013). Increased cover provided by vegetation and coarse woody debris gives small mammals more predator escape routes and more suitable foraging sites, facilitating an increased rate of acorn removal (Zollner and Crane 2003; Pérez-Ramos and Marañón 2008). However, increases in the availability of soft mast or other food sources after harvest (Perry et al. 2004; Reynolds-Hogland et al. 2006) provide small mammals with more alternatives to acorns. No changes in the abundance of small mammals occurred at our sites following midstory removal, but common granivores including the white-footed mouse (*P. leucopus*) and the eastern chipmunk (*Tamius striatus*) had a positive numerical response to the creation of harvest openings and associated edge habitat (Kellner et al. 2013). Because rates of hard mast removal were unchanged at edges, the larger small mammal populations must have used alternative food resources.

Isolating the impacts of different seed predators (white-tailed deer, gray squirrels, and smaller mammals) revealed that their impacts on removal were generally compensatory. When deer were excluded, the proportion of acorns removed increased, and when squirrels

were excluded removal did not decline greatly. This result suggests that the impact of deer and gray squirrel predation may not be critically important to oaks, because most seeds will eventually be removed by smaller granivores anyway. Deer are prolific consumers of acorns, particularly during the mast fall (McShea and Schwede 1993), but low deer density at our sites (Kellner, *unpublished data*) likely explains their low impact on removal. More important, however, is that equating acorn removal with predation is unwise when considering the impact of different groups of seed predators on successful oak regeneration. Secondary dispersal of acorns affects germination and seedling success, so removal is not unequivocally negative for acorn survival (Vander Wall et al. 2005; Moore and Swihart 2008). Scatter-hoarding mammals in particular make small caches of removed acorns that contribute to germination and seedling success if they are not later recovered (Smallwood et al. 2001; Steele et al. 2006). In contrast, acorns consumed by deer have no further chance of successful germination. So, even if removal is compensatory, changes in the relative abundance of seed predators could impact germination success.

Intact acorns were more likely to be removed than broken, weevil-infested, or germinated acorns (Table 3). The reduced nutrients in infested acorns and greater perishability of damaged and early-germinating acorns lowers their value for storage. Though these acorns may be removed and eaten immediately by predators, they also are less likely than intact acorns to be cached (Hadj-Chikh et al. 1996) and so their germination probability is reduced.

Conclusions

Considering the effects of seed predators on oak regeneration is crucial for oak forests of North America, Central America, (Lopez-Barrera et al. 2005) the Mediterranean region (Pérez-Ramos and Marañón 2008), and Asia (Maeto and Ozaki 2003). The results of this study confirm that pre- and post-dispersal seed predators, including both insects and vertebrates, have an important influence on the proportion of acorns that ultimately have a chance of germination and establishment. The effects of seed predators are most evident in years of poor mast production, when nearly all acorns produced were infested or removed. Timing harvest cuts for oak management to coincide with a sufficient amount of suitably sized advance oak regeneration is a challenge given the high variation in acorn production and predation. However, we observed the lowest levels of infestation and removal following very large mast crops, emphasizing the importance of planning a harvest for several years after a large acorn crop in order to generate a large cohort of oak advance regeneration. Acorn survival will also be higher when small mammal populations are low (Dey et al. 2008).

The relationship between oaks, acorns, and seed predators was not greatly changed by either midstory removal associated with a shelterwood harvest or the creation of clearcut openings. Following midstory removal, the only change observed was a reduction in weevil infestation, which likely has a positive effect on oak regeneration. All other things equal, an increase in the proportion of sound acorns following midstory removal should increase the amount of advance oak regeneration established prior to the removal of the overstory trees in the final stage of a shelterwood harvest. With regard to edges created by harvest openings, seedlings established from acorns produced by edge trees will not play a role in regenerating oak within the adjacent opening, because only larger advance regeneration will be competitive (Sander et al. 1984). However, changes in predation along edges can influence advance regeneration in the surrounding intact forest (Lopez-Barrera et al. 2005). Our findings indicate that changes in seed predation induced by opening edges were minimal,

which suggests that effects on advance regeneration in areas adjacent to openings should not be impacted negatively.

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